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***Paraphysoderma sedebokerense*, gen. et sp. nov.,
an aplanosporic relative of *Physoderma* (Blastocladiomycota)**TIMOTHY Y. JAMES^{1*}, YORAM HOFFMAN², ALIZA ZARKA² & SAMMY BOUSSIBA^{2†}¹*Department of Ecology and Evolutionary Biology, University of Michigan
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ABSTRACT — A monocentric blastocladialean fungus was identified as a parasite of the green alga *Haematococcus pluvialis* in aquaculture and isolated into pure culture. Phylogenetic analysis suggests the fungus is a sister taxon to the obligately biotrophic plant parasitic genus *Physoderma*. The parasite, which has not been observed to reproduce by zoospores, instead forms amoeboid aplanospores. We formally describe the new genus and species *Paraphysoderma sedebokerense* to accommodate this unusual member of the *Blastocladiomycota*.

KEY WORDS — algae, *Blastocladales*, cultures, nomenclature

Introduction

A fungal parasite of the green alga *Haematococcus pluvialis* has recently been characterized (as “*Haematococcus* parasite” in Hoffman et al. 2008) and provisionally referred to as “*Paraphysoderma sedebokerensis*” (Gutman et al. 2009; Porter et al. 2011). The parasite has the appearance of a typical chytridiomycete zoosporic fungus with an epibiotic globular sporangium subtended by an intracellular rhizoidal system. It was first observed during aquaculture of *H. pluvialis*, an important producer of the carotenoid astaxanthin used in cosmetics and pharmaceuticals (Del Campo et al. 2007). Neither pure nor dual cultures of the alga and fungus produced a zoosporic stage; instead sporangia released amoeboid aplanospores that were infective to *H. pluvialis* (Hoffman et al. 2008) but not other green algae (Gutman et al. 2009). In a molecular phylogeny based on the 18S ribosomal RNA gene the novel parasite was closely related but clearly basal to the plant parasitic zoosporic fungus *Physoderma* (*Blastocladiomycota*) (Hoffman et al. 2008). Its phylogenetic

position, the absence of a zoospore stage, and its occurrence in an algal host suggest that the parasite should be placed in a separate genus.

A detailed description of the infection cycle and growth characteristics of the parasite has been published (Hoffman et al. 2008). The goal of this paper is to provide a formal description of the parasite.

Taxonomy

Paraphysoderma Boussiba, Zarka & T.Y. James, gen. nov.

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Sporangium monocentricum, eucarpicum, epibioticum. Aplanosporae paucae usque ad plurimae per sporangium, sine flagellis, congregentes antequam liberati, per incisuram in sporangio exeuntes, 3–6 µm diametro pseudopodiis filosis, in superficie cellulae nutriticis repentes antequam incystati et endogene evolventes. Systema rhizoidale e puncto unico in sporangio evolvens, intra hospitem bulbosum. Sporangium dormiens epibioticum, fuscatus, pariete crassiore quam zoosporangium, germinans ut aplanosporas liberarent. In alga viridi parasitica.

TYPE SPECIES — *Paraphysoderma sedebokerense* Boussiba, Zarka & T. James

ETYMOLOGY — The new genus is closely related to, but distinct morphologically and in host preference, from the genus *Physoderma*.

SPORANGIUM monocentric, eucarpic, epibiotic. APLANOSPORES few to dozens per sporangium, lacking flagella, swarming before being released, exiting through tear in sporangium, 3–6 µm diameter with filose pseudopodia, crawling on surface of host cell before encysting and developing endogenously. RHIZOIDAL SYSTEM developing from single point on the sporangium, forming an apophysis inside host. RESTING SPORANGIUM epibiotic, darker and with thicker wall than zoosporangium, germinating to release aplanosporae. Parasitic on green algae.

Paraphysoderma sedebokerense Boussiba, Zarka & T.Y. James, sp. nov.

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Descriptio ad genus. In Haematococcus pluvialis parasitica.

HOLOTYPE — Hoffman et al. 2008, Mycological Research 112: FIG. 5D.

ETYMOLOGY — Referring to Sede Boker, Israel, the locality where the species was originally isolated.

Description as for genus. Sporangium size 20–35 µm in dual culture on host (Hoffman et al. 2008); aplanosporae with numerous refractive globules that coalesce upon encystment; parasitic on non-motile *Haematococcus pluvialis* Flot. (*Haematococcaceae*, *Chlorophyceae*).

Discussion

Paraphysoderma is differentiated from *Physoderma* by the absence of a motile spore, the presence of an epibiotic resting sporangium, culturability,

and host range. However, it has a general appearance of a typical monocentric, eucarpic chytrid or blastocladialean fungus, and is similar to *Physoderma* in having an epibiotic sporangium and a limited rhizoid emanating from a single axis on the sporangium. Its phylogenetic position (Hoffman et al. 2008) implies that the genus or species has recently lost a flagellated spore stage. Despite the absence of a motile spore, the aplanospores of the parasite are nonetheless able to cause severe epidemics in aquaculture.

Our current observations do not exclude the possibility that additional study of *Paraphysoderma* will ultimately reveal a zoospore stage. When sexuality is observed in members of phylum *Blastocladiomycota*, an alternation of diploid and haploid generations is observed (James et al. 2006). Thus it is possible that a thallus or stage of different ploidy on an alternative host may exist, although infection studies suggest it is not likely to be another green alga (Gutman et al. 2009). However, the observation that the aplanospores from both resting and thin-walled sporangia are morphologically similar suggests the absence of a separate gametophyte stage. If the fungus conforms to the life cycles expected of other blastoclads, then it would be considered to have a 'Brachyallomyces' (short) life cycle, which may or may not include meiosis during resting sporangial germination (Emerson 1941). The basal placement of *Paraphysoderma* to *Physoderma* is consistent with the derivation of the land plant parasitism from an aquatic one between a chytrid-like fungus and an alga. The culturability of *Paraphysoderma* and not *Physoderma* is consistent with the evolution of an increasingly obligate parasitic relationship of *Physoderma* to its host. Indeed, *Physoderma* and *Paraphysoderma* are unique among *Blastocladiomycota* in its parasitism of the plant kingdom, although whether the use of plant hosts is a derived or ancestral trait is unclear, as *Physodermataceae* occupy the most basal branch in the *Blastocladiomycota* (Porter et al. 2011). The distinct differences in culturability between the two genera suggests that *Paraphysoderma* might serve as a model species for the clade in research requiring large numbers of cultured cells, such as genomics and biochemistry.

The unique nature of the amoeboid swarming aplanospores suggests that neither genus nor species has been observed before. *Chytridiomycota* species that have been found to reproduce solely by amoeboid aplanospores include *Amoebochytrium rhizidioides* Zopf (host: *Chaetophora elegans* (Chlorophyceae)), *Sporophlyctis rostrata* Serbinow (host *Draparnaldia* spp. (Chlorophyceae)), and *Sporophlyctidium africanum* Sparrow (host *Protoderma* sp. (Ulvophyceae)), all of which differ in several ways (including rhizoidal development) from *Paraphysoderma*. An aplanosporic mode of reproduction is unusual among aquatic fungi, and the factors that favor the loss of a flagellated spore in an aquatic environment are unclear. The pattern that many aplanosporic chytrids parasitize green algae suggests that the need for a motile spore may be minimal

in certain well-mixed environments, while the ability to creep over the host to find an ideal location for rhizoidal penetration may be the trait most influenced by natural selection.

The number of accepted species of *Physoderma* is ~50 (Kirk et al. 2008). The number of species and distribution of *Paraphysoderma* are currently unknown but will probably be much greater than currently appreciated given the rapid expansion of chytrid diversity seen in both culture studies and environmental DNA surveys (Letcher et al. 2008; Freeman et al. 2009).

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